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STUDIES OF GASTROPODA.

AMADEUS W. GRABAU.[1]

MARINE gastropods appear to have reached their acme of development in the present geologic period. What the Jurassic and early Cretaceous time was to the cephalopods, the Tertiary and present periods are to the gastropods. This is indicated not only by the great number of species, but also by the fact that so many series have branched out into bizarre types, in which excessive development of spines and tubercles suggests that the limit of variation is approached.[2]

Phylogerontic types are furthermore to be found in the majority of series, while some groups, such as Strombus, Cypræa, etc., are represented only by phylogerontic forms in the modern seas.

[1] The author has for the past five years been engaged in the study of the phylogeny of gastropods, particularly the Fusidæ and some related types. A monograph on Fusus and some of its allies is ready for the press, while another, dealing especially with Fulgur and its allies, is in preparation. The present paper is intended as a contribution to the principles of study of the molluscan shell as applied to Gastropoda, principles first worked out for the Cephalopoda by the late Prof. Alpheus Hyatt and some of his contemporaries, and for the Pelecypoda by Prof. R. T. Jackson.

[2] See Beecher, Origin and Development of Spines, *Amer. Journ. of Sci.*, Ser. 4, vol. vi (1898), pp. 329–359; also *Studies in Evolution*, pp. 93 *et seq.*, Scribner, 1901.

The Protoconch of Gastropods. — The apical whorl of a gastropod shell has come to be generally known as the protoconch, though this term had been preoccupied for the corresponding apex of cephalopod shells. The protoconch of gastropods is essentially different from that of cephalopods in that it is (at least in the majority of types) twisted into one or more coils of a spiral nature, whereas that of cephalopods, so far as known, is a mere swollen bulb. The earliest portion of the gastropod protoconch agrees essentially in form with that of the cephalopods (Spirula, Ammonoidea) and pteropods, but spiral coiling appears very early in the majority of forms. Thus the protoconch of the Gastropoda may on the whole be considered as more specialized than that of the Cephalopoda. It might perhaps be thought desirable to dignify this specialized type of protoconch by a distinct name, as has been done by Jackson in the case of the pelecypod protoconch ("prodissoconch"). If so, the name "protorteconch," suggested to me by the late Professor Hyatt, would be most applicable. The shell or conch of gastropods may be specifically described by the term "torteconch," a name also used for the spirally coiled shell of cephalopods (Turrilites, Trochoceras).

The characteristics of the protoconch of most living gastropods are very variable, as might perhaps be expected in a class whose living members are on the whole highly specialized. Even in Tertiary times this specialization of the protoconch is noticeable. It is not always possible to determine the precise line of demarcation between protoconch and conch, since in a large proportion of types the two grade into each other imperceptibly. In certain types (Buccinum, etc.) a line and a slight change in the growth of the shell indicate the place where we may most reasonably make the separation between protoconch and conch. In a number of cases (Fusus, Hemifusus, certain Murexes, etc.) the end of the protoconch is strongly marked by the existence of a pronounced varix and an abrupt change of ornamentation (Fig. 5). In the majority of cases, however, no

FIG. 1. — *Rhopalithes rugoides* nov. gen. et sp., showing a fusoid (bulbous) protoconch with riblets on last portion and an abrupt beginning of the conch. Eocene. Paris Basin. × 10.

such definite line of demarcation exists. In general, the protoconch coils in the same direction as the conch, though conspicuous exceptions to this rule are found in Pyramidellidæ and other groups.

The early whorls of the protoconch of gastropods (except such ovoviviparous types as Cymbium) are smooth rounded coils of the type found in adult Natica, and best exemplified by *Lunatia heros* of our northern coast. In the majority of cases the initial whorl is minute, while the succeeding ones enlarge gradually and regularly. In some types the initial whorl is large and swollen (Fusus, Hemifusus, Fulgur, etc., Figs. 1, 7), when it is generally more or less elevated and oblique, a feature carried to excess in certain volutes. This type of protoconch has been termed "bulbous" by Dall.[1]

FIG. 2. — *Clavilithes rugosus* (Lam.). Eocene. Paris Basin. The apical whorls × 10, showing papillose protoconch and early conch whorls.

Again the initial whorl may be compressed so as to produce a conical form, the sloping sides of which are flat. This type, observable in so-called Clavilithes from the British and American Eocene and in some other genera, may be denominated a "trochoid" type of protoconch.[2] The flattening may be confined to the apical whorl or may be continued over one or more of the succeeding whorls. The normal naticoid type of whorl may continue, with regular increase, thus giving rise to the large "Melo" type of protoconch (Dall) so prominent in Melo and some other genera. When the whorls become depressed so as practically to lie in one plane, a "planorboid" protoconch is produced (Dall). Again the naticoid initial whorl may be succeeded by a number

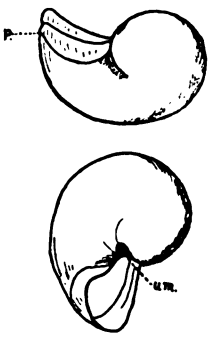


FIG. 3. — Protoconch of *Sycotypus canaliculatus*. *p*, end of protoconch; *um*, umbilicus. × 14.

[1] *Trans. Wagner Free Inst.*, vol. iii (1890), p. 67.

[2] The "trochiform" type of protoconch of Dall is more comprehensive, including the naticoid type.

of whorls which increase slightly or not at all in size, thus giving a long and slender type of protoconch which Dall has called "pupiform." This type of protoconch is characteristic of Clavilithes of the Paris Eocene (Fig. 2), of many Eocene and recent species of Turbinella, and of other forms.

The trochoid type of protoconch is apparently a case of specialization, and is confined to a comparatively small number of gastropods.

The naticoid initial whorl of the protoconch, so far as has been observed is umbilicated. This is well shown in Fulgur,

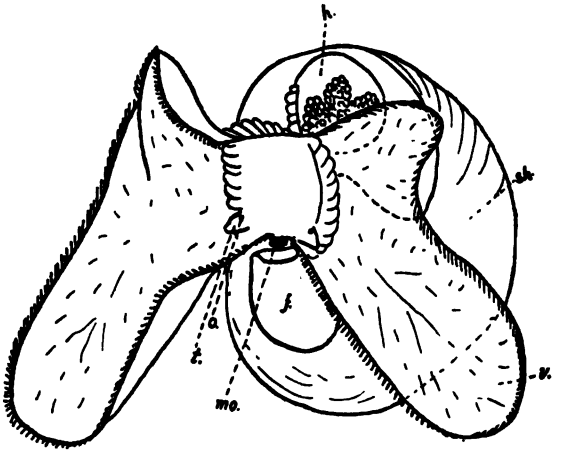


FIG. 4.—*Sycotypus canaliculatus* in the phylembryonic stage. *f*, foot; *h*, heart; *mo*, mouth; *o*, eye; *sh*, shell (protoconch); *t*, tentacle. × 30.

Sycotypus, Fasciolaria, Buccinum, and other types in which the initial whorls are large enough to be readily examined. The umbilicus is best shown in young individuals which have just completed the early protoconch stage (Fig. 3). It is well marked in Fulgur at the end of the protoconch (phylembryonic) stage, before the velum is fully developed (Fig. 4). This latter persists until just before the animal leaves the egg capsule, by which time the young conch has begun to develop and the umbilicus is closed. I believe that we are warranted in assuming that the umbilicus exists at some stage in the protoconch of the majority of gastropods, though it is conceivable that in extremely accelerated types, even this — apparently the most

primitive condition of a coiled protoconch — is lost. From the characters of the initial whorls of the protoconch we may argue that the radicle of the coiled gastropods must have been a naticoid type with a well-marked umbilicus. Such a type is found in *Straparollina remota* Billings, one of the earliest coiled gastropods of the Etcheminian or Lower Cambrian of the Atlantic border province of North America. That it is probably not the most primitive type of gastropod is suggested by the consideration that the earliest stage (ana-phylembryonic) of the protoconch is not coiled, but rather cap-shaped like modern Patella. Such primitive types are found in Lower Cambrian species which have variously been referred to Platyceras, Scenella, or Stenotheca, owing to the want of sufficient characteristics to define their exact relations.

Our modern patelliform shells are probably not primitive types, as shown by the protoconchs of Acmæa and Crepidula, which are coiled.

FIG. 5. — *Hemifusus colosseus* Lam. Recent. Apical whorls × 4, showing oblique bulbous protoconch with riblets in the last portion, and the abruptly beginning, accelerated conch with the shoulder developed at the beginning.

Ornamentation of the Protoconch. — In a number of species of gastropods the later whorls of the protoconch are ornamented by riblets (Figs. 1, 5), and more rarely by true revolving lines or spirals. In others a carina appears on the whorls of the protoconch.[1] These structures normally belong to the conch, where their strength and variation constitute the chief features by which the whorls are characterized. Their occurrence on the protoconch is due to a backward pushing of the normal conch characters, until they appear on the final whorls of the protoconch. This is in conformity with the law of tachygenesis, or acceleration in development, which is the key to the understanding of the taxonomic values of shell characters in

[1] For an account of the characteristics of the protoconchs of a number of gastropods, see Baker, F. C., On the Modification of the Apex in Gastropod Mollusks, *Ann. N. Y. Acad. Sci.*, vol. ix (1897), pp. 685–704, Pls. XVIII–XX; also *Proc. Phil. Acad. Sci.* (1890), pp. 66–72; (1894), pp. 223–224; *Roch. Acad. Sci.* (1891), pp. 130–132.

gastropods. Such accelerated type of protoconch is particularly characteristic of the Fusidæ, though not confined to them. In some members of this group, *i.e.*, *Fusus caloosaensis* and its congeners, the ornamentation of the protoconch begins very early, showing extreme acceleration. This is also true of *Fusus apicalis* Johnson. Neither of these species is a true Fusus.

The classificatory value of the protoconch of gastropods has not generally been recognized, Dall, so far as I know, being the only author who has made extensive use of it. It is, however, apparent that if our classification is to express genetic relationship, this, the earliest formed portion of the shell, demands a careful consideration. It is generally conceded that organisms of a common ancestry are more nearly alike in their earliest stages of development, differentiation becoming more and more marked in later stages. This is to be expected if the law of recapitulation of ancestral characters is accepted, for then the earlier stages must more nearly represent the features of the immediate ancestor in any particular restricted group. Furthermore, the smaller the taxonomic group, the more nearly identical must be the earlier stages, since in a small group the members have not become widely separated from their common ancestor. Thus, while the initial whorl of the protoconch does not differ widely, except in size, in the majority of gastropods, indicating the characters of the more distal radicle of the class, — *i.e.*, the naticoid ancestor, — the whole character of the protoconch must be considered in the determination of the more immediate relationships. Therefore, I believe it is not too much to say that the protoconchs of all the species within a given genus should agree as to their essential characteristics, and that no species can be considered congeneric in which the protoconchs show a radical difference. Thus, as will be shown in a forthcoming memoir on Fusus and some of its allies, the American Eocene species of Fusus do not show the typical Fusus protoconch, but some have a protoconch like that of many species of Pleurotoma and like *Levifusus trabeatus* (*i.e.*, *Fusus meyeri*, etc.). Others again have the protoconch of Fulgur (*Fusus quercollis*, etc.), of which group they are the Eocene ancestors. The species referred to have adult

conch features closely similar to those of Fusus, and the consideration of these alone has caused them to be placed in that genus. (Compare Fig. 6.) These examples, however, are due to parallelism rather than close genetic relationships. Great similarity exists between the protoconchs of Fusus and Hemifusus, thus showing a close genetic relationship between these two genera, while on the other hand Fasciolaria appears to be more widely removed.

Septa in the Apex of Gastropods. — Gastropoda in which the spire of the shell is long, generally develop septa near the apex. These septa partition off the protoconch and earliest whorls of the conch, and they may generally be seen in specimens with broken apices. Turritella, Cerithium and its allies, Fusus, and in fact turreted shells in general show this septum. It is generally a curved, more or less funnel-shaped element, though often only meniscus-shaped. The septum is invariably convex backward, as might of course be expected. The apical portion is generally uniformly curved and lies freely in the cavity of the protoconch or early conch. Septa are sometimes very numerous as observable in longitudinal sections (Triton, etc.), but generally the number is comparatively small. The septa are entirely imperforate and mark the withdrawal of the apical portion of the coiled visceral hump from the apex of the shell and the cutting off of the useless space by a partition wall. In a number of types the portion of the shell thus divided off becomes invariably broken away. An interesting type of structure which belongs here is found in the recent *Scaphella magellanica* Sby. and some related forms. In this, according to Dall,[1] "the larva is clothed with a cuticular or horny protoconch, probably similar in form to that which when shelly results in the 'bulbous nucleus.' Later on, but while still in

FIG. 6. — *Fusus asper* Sow. A typical primitive Fusus. Eocene. England. × 1½.

[1] Dall, W. H. Blake Gastropoda, *Bull. Mus. Comp. Zoöl.*, vol. xviii (1889), p. 452; *Proc. U.S. Nat. Mus.*, vol. xii (1890), p. 311, Pl. IX, Figs. 5, 6; *Trans. Wagner Free Inst. of Sciences*, vol. iii (1890), p. 67, Pl. VI, Fig. 5.

the ovicapsule, the deposition of limy matter begins as a slender cone or elevated point along the line of the axis of the protoconch, and as the larva grows the posterior part of the mantle secretes a shelly dome. Being thus cut off from the horny protoconch, the latter falls into shreds and is lost. The nucleus of the larva, still in the ovicapsule, then presents a slightly irregular dome, with a slender point rising from the apical part." To this apical point Dall has applied the term "calcarella." In this case the protoconch proper was horny and deciduous, while the first formed septum was calcareous and hence came to take the place of the protoconch when this was lost. Probably the types of nuclear whorls named by Dall "Caricella type" and "Scaphella type" from characteristic genera are secondary septal deposits of this type, as already suggested by that author.

Characteristics of the Conch. — The simplest type of whorl of the gastropod conch (torteconch) is round and smooth, showing only the lines of growth. This type, which is virtually only a continuation of the primitive protoconch whorls, is seen in Natica and similar types, and in these the umbilication is generally retained. Omitting Pleurotomaria[1] and its allies, this type of gastropod is most characteristic of the Paleozoic strata, the chief modification being the elongation of the spire, thus producing a loxonemoid type.

FIG. 7. — *Fusus porrectus* Sow. Eocene. England. Apical whorls × 10, showing bulbous protoconch and characters of early conch whorls.

One of the earliest modifications of the smooth shell is the appearance of spirally revolving, more or less elevated lines and the formation of transverse elevated folds or ribs[2] (Fig. 7). Our observations are still insufficient to settle the question as to the order of appearance of these two types of ornamentation. Where both are present the ribs in most cases are the first to appear to the unaided eye, the spirals

[1] The development of Pleurotomariidæ and Bellerophontidæ, and of Euomphalus and other related genera, has been well described by Koken (*Neues Jahrb. für Mineralogie*, Beilage, Bd. vi, pp. 305–483).

[2] These ribs must be distinguished from varices, such as occur in Scalaria, Harpa, and Murex.

not appearing visible until some time after. On the other hand, fine radiating lines — the precursors of the visible spirals — are seen in the embryonic hyaline shell of Fulgur, etc., before it has become opaque by the deposition of secondary calcareous material (Fig. 8). It is most probable, however, that these fine thread-like markings are merely due to a change in the texture of the hyaline shell, corresponding in that respect to the primitive lines of growth, and are not equivalent to the elevated spirals, whose existence is due to a regular, though slight, plication of the mantle edge which builds the shell. If we adopt this view as the most probable one, the ribs, so far as my observations go, must be considered the first modification of the shell in the ribbed and spiraled forms. It is, however, by no means true that spirals do not appear until after the ribs have been formed. In a great many Paleozoic genera ribs never occur, while spirals are well developed. This is well exemplified in the Ordovician genera Cyclonema and Trochonema, the most primitive types of which (*i.e.*, *T.* (*Gyronema*) *liratum* U. and S., etc.) are umbilicated shells of a round-whorled or naticoid outline, with spirals more or less strongly developed. Among the earliest ribbed shells of naticoid form is *Holopea pyrene* Billings from the Middle and Upper Trenton group of Canada and central United States. The ribs are scarcely anything more than coarse undulations, very like the dying stages of the ribbed condition in more highly specialized genera of later geological periods. They have, however, the chief qualities of the ribs in their most accentuated development, and must be regarded as such. As nearly as can be determined from the illustrations given by Ulrich,[1] the earliest stages are free from undulations, thus indicating that, as we

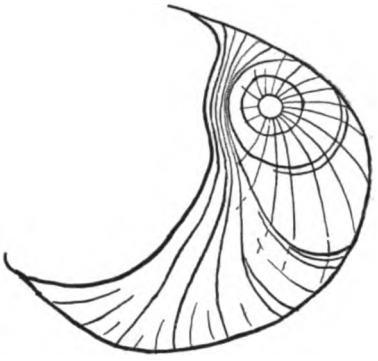


FIG. 8. — Early hyaline shell of Fulgur (Sycotypus), showing primitive lines of growth and fine radiating lines. × 48.

[1] *Palæontology of Minnesota*, vol. ii, Pl. LXXIX, Figs. 13–18.

should naturally expect, the ribbed were derived from the smooth species which precede them immediately in time. The immature specimens of *H. pyrene* illustrated by Ulrich show well the faint beginning of undulations which become pronounced only in the adult.

A somewhat more specialized ribbed shell from another phylum is found in *Natica nexicosta* Phillips of the Devonian. This in form is truly naticoid, with the ribs sharp, narrow, and uniform, separated by uniform intervals which are much wider than the ribs. The earliest stages, as far as can be judged from the illustration,[1] are ribless. The whole aspect of the last whorl of this shell is strikingly like the final whorls of the protoconch of highly specialized Tertiary and recent gastropods. *Natica subcostata* Schl. of the Devonian (Stringocephalen Kalk) of Paffrath, Germany, is another example, in which the costæ or ribs have become compound, secondary shorter ones being intercalated between the longer ones. *Natica costata* from the Lower Trias of St. Cassian carries the simple type of costæ into the Mezozoic era, while *N. armata* from the Upper Trias of that region shows the further complication of revolving spirals which are cancellated by the sharp ribs. In the later forms generally the umbilicus is closed. A similar succession of smooth, simple-ribbed, and cancellated-ribbed shells appears in Jurassic Nerita and Neritopsis, as illustrated by Hudleston in his monograph of the "Inferior Oölite Gastropoda."[2] Among the turreted types simple ribs appear in some of the Devonian Loxonemas, some species of this genus showing the further specialization of cancellating spiral lines. Similar successions may be found in a great many other series, and it is perhaps not too much to say that in the majority of the larger phyletic series, except those highly specialized, the radicle is a smooth, round-whorled form, succeeded by types in which the adults are ribbed, and later cancellated, after which progressive modification may be carried further. The index to the history of the phylum is in general to be found in the life history of the individual member under consideration as revealed

[1] Whidborne. Devonian Fauna of the South of England, *Palæontogr. Soc. Mon.*, Pl. XIX, Fig. 1. [2] *Palæontogr. Soc. Mon.*, Pl. XXVIII.

by the succession of characters in the shell whorls, from the earliest (nepionic) conch stage to the adult (ephebic) stage.

The revolving elevated lines, or "spirals," may in general be considered as primary and post-primary. The primary ones are the first to appear, and they increase in number by the exogenous appearance of new ones on the upper and lower portions of the whorl, outside of those which appeared first. Secondary spirals appear *between* the primary ones as these diverge, owing to the uniform increase in size of the whorls. Tertiary spirals and spirals of a higher cycle appear in specialized forms, but all such forms begin with only primary spirals, and generally only a few — sometimes even only one of these. The higher cycles come in later progressively, being most numerous in the adult stage. This teaches us that in the primitive type of a series we may expect to find primary spirals only, even in the adult, and experience shows that these are characteristic of the earlier members of any series, and that they generally accompany simple ribs and simple rounded whorls. (See Figs. 6 and 7.)

The first modification in the form of the whorls in gastropod shells is generally a change from the primitive rounded outline to an angular one, which causes the division of the whorl by a median or submedian keel, or carina, into an upper, more or less flattened "shoulder" portion and a lower, generally larger body portion (Fig. 5). Sometimes more than one carina arises, in which case all except the lower portion of the whorl becomes flattened, the section assuming the appearance of a portion of a polygon. The angulation, which finally develops into a carina, and often into a more or less accentuated "keel," is generally due to the strengthening of one of the primary spirals above the others. When the shell is ribless the angulation becomes a smooth keel. This feature appears early in the pleurotomarioid shells, in which the angulation is generally accompanied by an emargination or sinus of greater or less depth, which occupies the place of the carina. This group of shells, which appears to be a very heterogeneous one, probably had its beginning in the Lower Cambrian species of Raphistoma, of which *R. attleborensis* Shaler and Foerste is

the representative in the Etcheminian limestones of the Atlantic coast region. That this species is derived from th round-whorled *Straparollina remota* of the same horizon seems probable on comparison of the species, and this is in line with the theoretic consideration which derives the angular-whorled forms from more primitive round-whorled species.

When the angulation appears far down on the whorl, so that the suture of the next whorl touches it, a trochoid shell is produced, which varies in outline from the gently tapering form of many Cerithiums, etc., where the basal angle is very obtuse, through the flat-based Trochus, where the angle is strongly acute, down to Xenophora with concave base and overhanging lateral margins, where the acuteness of the angle is extreme.

When the angle is relatively far up on the whorl, so that the body portion is the largest, we have again two types of spires produced. When the succeeding whorl joins the earlier one *below* the angle, a turreted or terraciform spire is produced, in which the length and slenderness of the spire depends on the amount of the embracing of the whorls and the obtuseness of the shoulder angle. The long graceful spire of *Fusus toreuma* and its near allies is a result of a pronounced slope of the shoulder, together with a very moderate degree of embracing of the whorls, or what might be called a slender coiling. The strong contraction of the body of the whorl below the angle accentuates the slenderness of the spire, producing what is generally called a depressed suture. In some other species of Fusus all these features are less accentuated, and the spire as a result becomes more condensed and relatively stouter, thus losing some of its gracefulness. In other gastropod shells we can study all degrees of condensation of the spire owing to the increased embracing of the whorls, the flattening of the shoulder even to right angles with the axis of the spire, and the assumption of a cylindrical form by the body of the whorl. When the later whorls embrace the preceding ones up to the shoulder angle, a uniformly sloping trochoid spire is produced, the degree of slope of which depends on the angle which the shoulder makes with the longitudinal axis of the spire. Thus we may have every gradation from the long slender spire of certain

pleurotomoid shells to the perfectly flattened or even slightly sunken spire of certain species of Conus. In this latter genus it is perceptible that even in the most flattened species the young whorls form an elevated spire, which varies in intensity of slope in different individuals. The flattened or sunken condition appears only in the later stages.

A type of modification of the whorl, which at least in appearance belongs here, is due to the formation of a notch in the

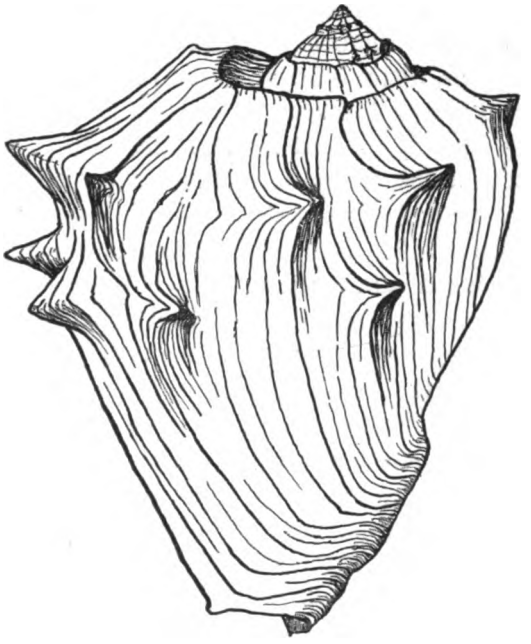


FIG. 9. — *Melongena melongena*. An immature individual, showing the melongenoid growth and the spines. Slightly reduced.

posterior margin of the aperture of the shell, where the body whorl joins the preceding one. This feature has so far been found only in the old-age stage of the individual, or in the adult or even earlier stages of phylogerontic types, *i.e.*, such as belong to a declining group of gastropods. This posterior notch may cause a transgression of the final portion of the last whorl on the spire, thus covering up a portion of the preceding whorls. This is generally accompanied by a resorption of previously formed spines or other ornamentation which would

interfere with the comfort of the animal. Accompanying the formation of this notch is generally a change in the outline and ornamentation of the last whorls, as will be discussed further beyond. This type of structure is well shown in *Melongena melongena* (Fig. 9) and *M. patula* of the modern tropical seas, and may well be termed a "melongenoid" type of growth. A striking modification of this type is seen in Strombus, where it appears only in the adult and is accompanied by the formation of a lip, and by fingers in pteroceroids.[1] This may be termed a "stromboid" type of growth. It appears periodically in Cassis, where it has the value of varices. An extreme type, the "cypræoid," is seen in Cypræa and Ovulum, where the spire is entirely covered in the adult. Still another type, characteristic of the Eocene Clavilithes and related genera, is produced by the flattening of the top of the posterior canal and the production of a flat sutural shelf, which however is unaccompanied by an increase in the amount of embracing of the whorls. This shelf thus runs like a regular spiral path around the spire part way, in rare cases almost all the way, up to the apex. This type deserves to be specified as the "clavilithoid" type of growth. In extreme cases it spreads out laterally into a flange, which in certain species is broken up into blunt, vertically flattened spines (Fig. 18).

One of the most pronounced modifications of the aperture is the formation of an anterior notch at the point most distant from the apex. This notch which lodges, and is due to the formation of an anterior mantle fold which serves the purpose of a siphon, is in many specialized types drawn out into a long slender canal, which finds its most perfect development in Fusus and in certain Murexes, where it is occasionally transformed into an almost closed tube, from the apposition of the upper borders. This type of modification makes its appearance in the Ordovician genera Subulites and Fusispira, where, however, the canal is more suggested than actually developed.

Ornamentation of the Whorls. — The simplest types of what for want of a better term we may call ornamentation of the

[1] From unpublished studies on Strombidæ, by Miss I. H. Ogilvie, it appears that the Pterocera has a polyphyletic origin.

whorls are, as already suggested, simple ribs, or spirals, or both. When the whorls remain round throughout the life of the individual no other regular ornamentation is as a rule produced, except that in the final (gerontic) portion of the last whorl the ribs, and in some cases the spirals, may disappear, leaving the shell smooth. If, however, a shoulder is produced through the formation of an angulation, a new succession of ornamental types will arise, which generally appears in the same sequence in widely separated groups of gastropods. The first effect of the angulation seems to be to concentrate the growth force on it. The ribs become accentuated on the angle, and correspondingly fainter away from it. Finally, they disappear above and below the angle, being represented on the latter, however, as a series of tubercles. These tubercles, though generally blunt, may at times assume a somewhat spinous form; but they appear to be distinct from true spines, which, so far as observed, are a feature of later growth. In the cases in which actual succession has been traced out in series (Fulgur, Fusus, Hemifusus, etc.) it was found that the knobbed or tuberculated stage is succeeded by a stage in which the tubercles become confluent, producing a pronounced ridge or keel on the angulation. This after a time disappears, and with it the angulation, the outline of the whorl becoming rounded again, with only the spirals persisting. These in some cases may disappear also, or at least become very faint. After the whorl has returned to its primitive rounded outline a new type of modifying element arises in the form of spines. These begin as notches in the margin, generally in the spiral zone of the angulation of the earlier whorls, but sometimes in a second or even a third zone lower down on the body of the whorl (*e.g.*, Melongena). They mark a distinct and periodic fold in the outer lobe of the mantle, which sometimes is accompanied by a temporary cessation in shell building, as indicated by more or less strongly marked resting lines in the lines of growth of the shell (*Fulgur carica*, etc.). They thus have all the characters of varices of the type so pronounced in Murex, where their multiple development and frequent compound character produce the most striking feature of the group of shells generally associated

under that generic name. When the spine has been fully developed, the fold in the mantle which caused it may gradually diminish in size, with the active resumption of the shell-building process, until it finally disappears. In this case the spine is gradually closed on the apertural side, thus becoming symmetrically developed (Fulgur, Hemifusus). In some cases, however, the fold of the mantle appears to be lost abruptly when the shell-building process recommences. In such cases the apertural side of the spine remains open, becoming entirely external by the flooring over of the emargination produced by the spine in the shell margin. This type is most characteristic of the spines forming the varices of Murex.

Through a process in acceleration in development, which will be more fully discussed below, the spines may be crowded backwards, *i.e.*, appear earlier and earlier, thus condensing the preceding stages more and more until finally some of them are dropped out altogether. Thus it will eventually happen that as in *Fulgur carica* of the recent fauna the keeled and smooth stages are dropped and the spines follow immediately upon the tubercles, and to some extent even encroach on these. A gradual passage from the true tubercles to the true spines is thus produced, and it becomes practically impossible to determine where one type ends and the other begins. This feature may be readily observed in the various species of Hemifusus, in most of which varieties occur showing all stages from the widely separated tuberculated and spinous stages to those in which spines and tubercles grade into each other without allowing a line of demarcation to be drawn. In trochoid and other shells in which the whorls embrace up to the angulation, the spines, if present, are either imbedded in the succeeding whorl and more or less covered up, or else they are progressively resorbed as the new whorl increases. In Melo and some other genera the spines project upwards and are generally unclosed on the apertural side. This produces the spiral "corona," so striking a feature in some shells. Finally, the remarkable apical character of *Yetus* (*Cymbium*) *proboscidialis* should be mentioned. In this a depressed, smooth, central, apical area occurs, due to a secondary deposit which covered

up all the preceding whorls. This is margined by a sharp elevated and thin edge.

Varices. — Varices are the periodic rows of spines, or the reflexed or bent-over lips which mark recurrent stationary periods in growth in many gastropod shells. Several types may be recognized, — the spinous, *e.g.*, Murex, the simple reflexed lip, best shown in Scalaria, and the periodically accentuated normal rib, perhaps the most abundantly represented type. The simplest type of the spinous varix is that in which each stopping place is marked by only one simple spine. Such a condition, found in Fulgur and a number of other genera, is generally not considered as falling under this category; but it is clear that the multispinous varix is a modification of the unispinous one. This becomes more apparent when we note that in every multispinous varix one of the spines predominates over the others to a greater or less extent. On tracing back the spiral from which this spine arises, which is generally possible, even though the lower spines are progressively resorbed by the advancing inner lip of the new whorl, it appears that in every varix it bears the largest spine. Finally, on tracing back far enough, only one spine is seen on the whorl, — the primary spine, which throughout is recognizable by its predominant size. In *Murex brassica* Lam. of the west Mexican coast we have a type in which only a few additional small spines occur besides the primary large spine. This is but slightly advanced beyond the state found in Fulgur. In *M. bicolor* the shell continues to grow somewhat after the chief varix is formed, the principal spine alone remaining unclosed, so that the lip at the resting stage differs little from that of Fulgur. The multispinous type of varix, with simple spines, is best illustrated in the beautiful *Murex tenuispira* Lam., the most striking in form of all the Murexes. Each spine arises from a spiral line, of which it forms the apertural prolongation. The shorter spines arise from the secondary spirals, and on the canal they are bent at about 120° forward from the primary ones, thus lying parallel to the primary series of the next but one varix preceding. Only in the neighborhood of the large spine do the tertiary and even later cycles of spirals terminate in small spines.

If the spine from a primary spiral does not increase in length rapidly, but increases in width, the secondary and later spirals, instead of developing independent spines, encroach upon the primary one and modify it by the production of lateral crenulations, which, as the spine grows, diverge more and more and become more and more pronounced, until the striking multilobed character of the spine of *M. palma-rosæ* (Lam.) and other highly ornate species is attained. If the principal spine of such a species is traced backward through preceding varices (which can generally be done, since resorption does not reach up to it), it will be found to be less and less complex in earlier and earlier varices, and ultimately may perhaps — in a very perfect specimen — be resolved into a single spine. (See Fig. 10.) In the growth of the spine itself, from its beginning on the final or first varix (counting backward) to its full development, as already noted, it progressively increases in complexity. A stage somewhat earlier than the adult stage in this spine shows the same degree of complexity as the *adult* of the representative of this spine in the next preceding or second varix. A still earlier stage in the principal spine of the first varix corresponds to the stage just preceding the adult in the principal spine of the second varix, and to the adult stage in the corresponding spine of the next earlier or third varix, and so on. In the same manner, though less perfectly developed in most cases, the spine next below (anterior of) the principal spine on the final or first varix has the characters of the adult of the principal spine in the next preceding or some earlier varix, and the third spine has the adult characters of the principal one in a still earlier varix. The last spine of the final varix — presumably the last formed one — has the characters of the principal spines in one of the earliest varices, when the shell was still very young (Fig. 10, where *A-10* corresponds to *K-1*, and *B-10* to *L-1*). Thus each spine passes through a succession of stages, and in its reappearance in a new varix it has made marked advances. The life history, therefore, of a single spine may be read by noting the characters of all the spines of that varix progressively from the smallest to the largest. This also indicates in general the life history of the group to which the

species under consideration belongs. Thus in an ancestor of *M. palma-rosæ* we might expect that the principal spine on the last formed varix of the adult shell would have the characters of this same spine in an earlier varix in *palma-rosæ* or those of a more anterior spine in the adult varix of that species. Such correspondence of characters in localized areas (*e.g.*, a single varix), with the changes characteristic of the life history of the group, has been called by Jackson the formation of localized

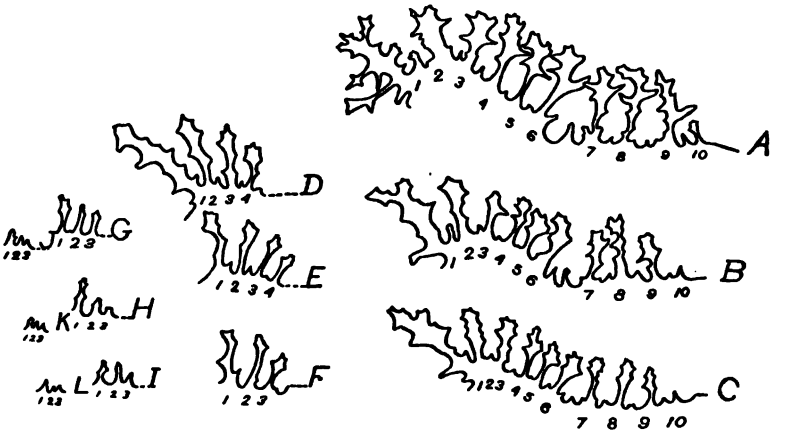


FIG. 10. — Diagram of the varices of *Murex brevifrons* Lam., from the West Indies. *A* is the last or most recent varix, *L* the earliest recognizable one. The corresponding spines are numbered alike. The dotted line indicates that the remaining portion has been resorbed.

stages in development, and he has found this phenomenon in a great many types of animals and plants.[1]

One of the commonest types of varix is that due to accentuation of normal ribs. Even in the spinous Murexes the bases of the spines are merged in such an accentuated rib, which recurs with greater or less frequency, though with regular periodicity, in the various species. This accentuated rib, whether spinous or not, appears to mark the periodic culmination of constructive vitality, after the expenditure of which a rest is necessary before building again commences.

The varices of Harpa are due to a periodic reflection of a smooth lip, which has the appearance of a margin rolled back.

[1] Jackson, R. T. Localized Stages in Development in Plants and Animals, *Mem. Boston Soc. Nat. Hist.*, vol. v, No. 4.

In Scalaria the varices are simple labial flanges, which stand out as sharp ridges, with the appearance of ribs. In *Helix albolabris* and other types the varix is formed only in the adult. In all types with successive varices it may be observed that the varices of the same longitudinal zone do not form a line parallel to the axis of the shell, but that this line runs spirally backward, in the direction opposite to that in which the whorls coil (Fig. 12). This is due to the fact that there is a progressive diminution in the proportional amount of building which was performed between the resting stages. If the amount of building were proportional to the size of the shell, the varices would run in straight, constantly diverging lines (Fig. 11) instead of spiral ones. If the proportional increase were too great for the size of the shell, and progressively increasing, the lines of varices formed by the corresponding ones of all the whorls would pass spirally forward, *i.e.*, in the direction of coiling of the shell. Neither this nor the case of increase proportional to the size of the shell has been noted, and it hence appears that we have here an illustration of Minot's law of senescence, the animal progressively growing old from the beginning. This feature is best shown in Scalaria, where in large specimens an additional feature, first pointed out to the writer by Prof. R. T. Jackson, is also seen. This is the more rapid shortening of the building stages, in the old age of the individual, so that the varices of the last — old age — whorl are not continuous with those of the preceding ones but fall between them, so that sometimes a varix may be the whole length of a period behind what it should be (Fig. 13). In phylogerontic species of Scalaria this feature appears in the adult or earlier whorls,

FIG. 11. — Diagram illustrating hypothetical varix growth, with uniform proportional increment.

FIG. 12. — Diagram of the characteristic retarded growth between varices.

which whorls will then have a larger number of varices than those preceding them.

Other Ornamental Features.—Dall[1] has demonstrated the purely mechanical origin of the columellar plication in gastropod shells to be due to the sliding inward and outward over the columellar surface of a mantle lobe folded by being crowded into too small a space. In Cypræa these plications are most numerous and developed in the adult on both sides of the aperture. The intensity of the plications varies with the nearness or remoteness of the muscle of fixation. In a like manner the liræ of the outer lip may be explained. We must, however, be careful not to mistake the strong spirals, which sometimes appear through the thin covering of the inner lip, for plications, or the interspiral spaces appearing prominently in the thin outer lip, for liræ. Countess von Linden has discussed at length the development of the color pattern in gastropods,[2] and the reader is referred to her paper.

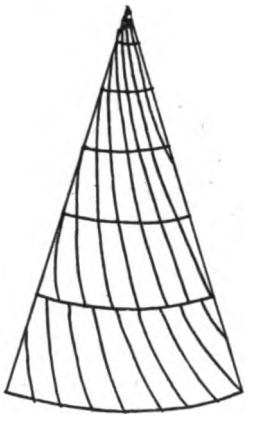


FIG. 13. — Diagram illustrating gerontic characters in the varices of the last whorl.

Individual Old Age, and Phylogerontic Characters in Gastropods. — Gerontism, or old age, is marked in its earlier stages in gastropod shells by the disappearance of features characterizing the adult. Such disappearance of features is generally in the reverse order in which they were formed. In the fusoid types the shoulder and the spines are the first to be lost, if they have been developed; or if there were only spinous tubercles, as in the Fusidæ, these disappear together with the angulation, and the gerontic lip becomes smooth except for the spirals. The normal outline is next more or less modified by an attempt at straightening out the whorl and making it more cylindrical,

[1] *Loc. cit.*, p. 58.

[2] von Linden, Maria. Die Entwicklung der Skulptur und der Zeichnung bei den Gehäuseschnecken des Meers, *Zeitschr. für wissensch. Zoologie*, Bd. lxi, pp. 261–317. 1 pl.

producing a consequent obscurity of the canal. The last stage in gerontism is observed in the loss of the power to coil, which is at first expressed in the separation of the inner lip from the columella; and if any further coiling occurs, in the loose apposition of the whorls and the consequent formation of an umbilicus. These features never go very far in the normal gerontic individual, for death intervenes and ends the process.

Among the highly specialized types of gastropods uncoiled phylogerontic species are relatively uncommon. Perhaps the most striking example in a highly specialized group in which such a want of regular coiling does exist in the adult is Vermetus. This, as is well known, has all the characters of a Turritella in its young stages, showing its derivation to be from that group. In the adult, however, it loses the power to form a regular spiral, turning and twisting in all directions and completely uncoiling at times, so as to make these portions of the shell almost indistinguishable from worm tubes such as Serpula. In primitive gastropods non-coiling, through the loss of the power to coil, appears to be the normal expression of old age, or gerontism, since in most cases the coil is the only feature which can be modified.

Shells with the final portion of the coil unrolled are well represented in the Ordovician. They even occur in the Cambrian, as indicated by *Platyceras primævum* Billings from the Lower Cambrian. From what is known of this little shell it appears that it represents a strongly umbilicated, low-spired naticoid type, with a portion of the last whorl free. If, as appears to be the case, the early whorls are normally coiled, and only the later coil loosely, this little shell represents the first phylogerontic type appearing side by side with the naticoid radicle of the entire group of gastropodous mollusks. Leaving out the loose coiling Eccyliomphalus and Eccyliopterus as of questionable affinities, the first well-pronounced example of a phylogerontic type with the final whorls not coiled is found in the Ordovician pleurotomarioid genus Lophospira. This genus, which comprises mainly normally coiled umbilicated forms, contains a few species which have become phylogerontic and show various degrees of non-coiling (Fig. 14).

Trochonema vagrans Ulrich and Scofield (Fig. 15), from the Stones River group, represents a phylogerontic type among the carinated naticoid gastropods, while *Dyeria costata* (James), from the Upper Lorraine of Cincinnati, represents a phylogerontic type of the group of simple naticoid shells with depressed spire. In the Silurian, *Platyostoma* (*Diaphorostoma*) *niagarensis* frequently shows individual gerontism by a loose outer lip. *Platyceras niagarense* represents a phylogerontic type, possibly derived from the former. In the Devonian the phylogerontic non-coiling Platycera abound. We find all degrees of coiling, from the close-coiled non-umbilicate Diaphorostoma, which appears with slight modifications throughout most of the series, to the straight "Orthonychia," which appears as a terminal member in most groups. Very often a number of species of "Platyceras" can be traced to a species of Diaphorostoma or Strophostylus occurring with them, the gradations being perfect. From such evidence it appears that the numerous species classed together as Platyceras must be split up into groups, each of which has been derived from a close-coiled ancestral species, probably within the same geological horizon. If so, the name Platyceras becomes meaningless for generic purposes. The great difficulty which besets the proper breaking up of what appears most certainly to be a group of polyphyletic origin lies in the small number of ornamental characters which can be made use of in tracing out relationships. In many Platycera spines appear, but these cannot be regarded as clues to affinity, since spinous types may and do arise in any group. What seems to be the right method of procedure was made use of in the

FIG. 14. — *Lophospira helicteres* var. *wisconsinensis* A. and S., showing loose coiling. (After Ulrich, *Palæontology of Minnesota*, vol. ii, pl. lxxii, Fig. 26.)

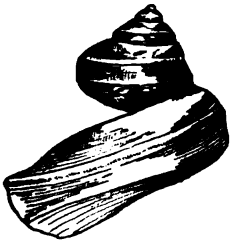


FIG. 15. — *Trochonema vagrans* U. and S., illustrating gerontic final whorl. (After Ulrich, *Palæontology of Minnesota*, vol. ii, pl. lxxviii, Fig. 13.)

determination of the genetic relation of *Platyceras arkonense* Shimer and Grabau, from the Hamilton of Ontario.[1]

Natica neritæformis, from the European Muschelkalk (Queenstedt), as far as can be judged from the internal molds which are alone represented, is a phylogerontic member of a simple naticoid group of shells. Fissurella, Acmæa, and other patelloid types, so common in the Mezozoic and modern sea, have, as already noted, a coiled protoconch. They therefore represent phylogerontic types, in which the power of coiling has been lost after the completion of the protoconch stage. In Crepidula the power to coil is still retained in a slight degree. In the majority of specialized gastropods phylogerontism is expressed, not in the non-coiling of the last portion of the spire, but in its expansion and wrapping about the earlier whorls so that these become more or less concealed. This is generally accompanied by the loss of all ornamental characters except, in some cases, the coloration. Sometimes it happens, however, that spines arise independently on this portion of the shell. This is most marked in Melongena and can be readily explained by the peculiar manner in which the shell develops.

In the young stage every typical Melongena has the characters of Hemifusus. In accelerated species of this genus spines follow the tubercles, the two grading into each other as in *Fulgur carica*. In other species, however, notably *H. colosseus* Lam. and *H. (Melongena) pugilinus*, a keeled or even smoothly rounded stage intervenes between the tubercled and spinous stages. (See *ante*.) This enables us to understand Melongena.[2]

The two typical species of this genus appear to have been derived from the same ancestral species, which coexists with

[1] Shimer, H. W., and Grabau, A. W. The Hamilton Group of Thedford, Ontario, *Bull. Geol. Soc. Am.*, vol. xiii, p. 176.

[2] Only the two typical species, *Melongena melongena* and *M. patula*, are referred to here. Most of the other species generally referred to this genus belong elsewhere. Such species as *M. morio* and *M. pugilina* are transitional from typical Hemifusus, *e.g.*, *H. colosseus* Lam., being produced chiefly by a condensation of the typical Hemifusus characters. They are generally classed with Melongena, but have not the typical phylogerontic growth of that genus. They will be referred to under both names.

them, — namely, *Hemifusus* (*Melongena*) *morio*. Representatives of this species occur in both west African and West Indian waters. From the west African type appears to have been derived the Mazatlan species *Melongena patula*, while *M. melongena*, at home in West Indian waters, was derived from the West Indian representative of *H.* (*M.*) *morio*. In both species the phylogerontic melongenoid form of whorl appears immediately after the tubercled and before the spinous stage, this latter coming in somewhat later. Thus, while the mode of coiling has become senile, the formation of the spines indicates

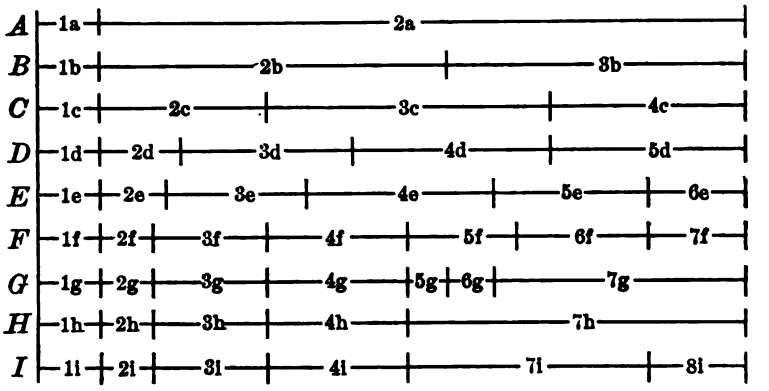


FIG. 16. — Diagram illustrating Hyatt's Law of Acceleration in Development. For description see text.

the persistence of one portion of the vigor of the adult. Such form of acceleration may be called partial or incomplete, differing in that respect from Fulgur, in which the acceleration is complete. A reason for this may perhaps be found in the following consideration: Fulgur is an accelerated type in the present fauna. The species in which a separation existed between the tubercles and spines all lived in Miocene and Pliocene times, and hence in the modern descendant (*F. carica*) spines have become firmly established. We may further suppose that the power to form spines has persisted so long that in the adult it is on the wane; and hence if any phylogerontic types of Fulgur should arise, the spines would first disappear and probably would never be formed again. In Hemifusus, on the other hand, the spine-forming power has

apparently been but recently acquired, judging from the frequent lateness in appearance of spines in individuals. Thus there would be more vitality or spine-forming power left, which would be able to overcome any weakening effect of senility appearing in other features of the group. Hence, though a gerontic form of coiling is assumed by the whorls of Melongena, the power to form spines is still retained, and these appear after an interval in the senile portion of the whorl.

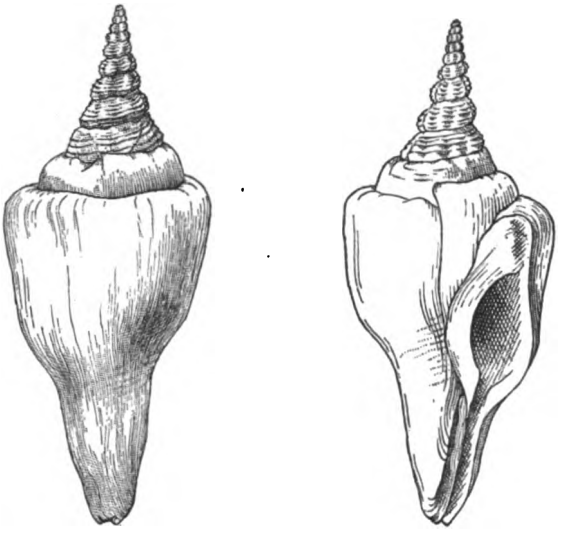
Illustrations of the Law of Tachygenesis and of Parallelism among Gastropoda. — Hyatt's Law of Tachygenesis, or acceleration in development, teaches us that the adult characters of a species are inherited at an earlier stage in the members of a succeeding generation. This of course implies a condensation of preceding characters, which in some cases may even be dropped entirely. The diagram on page 941 (Fig. 16) will give a clearer representation of the working of this law.

Let each of the lines *A* to *I* represent the life history of an individual gastropod in a phylogenetic series, beginning with *A*. Let the life history be divided into stages numbered from 1 up, each stage being characterized by some definite feature in the shell.

No. 1 is the protoconch stage, which persists throughout; No. 2, the smooth, round, whorled naticoid stage; No. 3, the primitive ribbed and spiraled stage; No. 4, the angular stage, with formation of nodes at the crossing of the ribs; No. 5, the keeled stage; No. 6, the second round-whorled stage; No. 7, the spinous stage; No. 8, the spineless smooth stage.

It becomes apparent that as new characters appear, the older ones persist for a shorter and shorter time. This is necessary, for otherwise each succeeding species must be larger to accommodate the new characters. This is acceleration by condensation. A character newly acquired in one member of the series appears earlier and earlier in the succeeding members of that series, thus changing from an adult to an infantile character. Some characters are less resistant than others, and these will be more quickly condensed. Such is the case with those of stages 5 and 6, the keel and the second round-whorled stage. The nodes are very persistent, and the

spines (of stage 7) are very vigorous. Thus it will happen, as in *H*, that stages 5 and 6 are dropped out altogether, stage 7, the spinous one, following upon stage 4, the tubercled



FIGS. 17 and 17 *a*. — *Cyrtulus serotinus* Hinds. Recent. A phylogerontic type of the Fusus series. Natural size.

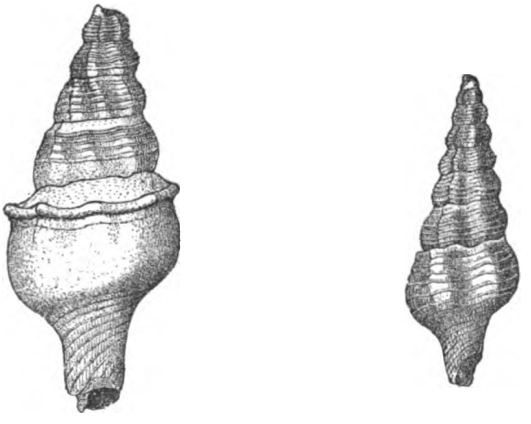


FIG. 18. — *Clavilithes chamberlaini* Johnson and Grabau. Eocene. Texas. Two stages; the adult showing a serrated flange and clavilithoid form. (*Proc. Phil. Acad. Nat. Sci.*, September, 1901.)

one, and even encroaching upon it. This is acceleration by elimination (example: *Fulgur carica*). Finally, even the vigorous spines disappear, and the final smooth gerontic stage is formed.

Parallelism. — There are perhaps few if any classes of invertebrates which equal that of the Gastropoda in illustrating the law of parallelism of development. In the Gastropoda similar features constantly arise independently in entirely distinct series; and since these features are generally used as a basis of classification, it follows that our present system of classification is in great need of revision. If we represent the natural system of classification by the customary tree and its branches, and then pass a more or less warped plane through the upper part of this tree, intersecting each branch at the same relative stage of development, we obtain a number of scattered points where the plane and the branches intersect. If we consider these points species, and group all the neighboring and perhaps some distant points into genera and so on, we will get very much what we have to-day in the classification of marine gastropods. In point of fact, we have only one episode in each of the large number of distinct phyletic series, and what we mistook for relationship is only a resemblance in a parallel developing series which has been cut at the same stage in development. Thus it is clear why the customary mistake of placing the recent *Cyrtulus serotinus* (Figs. 17, 17 *a*) with its parallel, the Eocene Clavilithes, is so generally made. Both are phylogerontic members of entirely distinct phyletic series, but they have reached the same stage in development. Again Fusus, known only in the Eocene of Europe, and in this country only from the Miocene on, has its close parallel in Pseudofusus and other genera in the American Eocene. Here the same type of form is developed, — a very simple matter, — but, as shown by the life history, the two types are widely apart genetically. Again, all gastropods with stromboid lips are placed with Strombus, a proceeding which has no warrant from a phyletic point of view. The common proceeding of classing all loose coiled or non-coiled Palæozoic gastropods under Platyceras has likewise no warrant from a phyletic view point, though it must be confessed that this is a convenient method when we do not know what else to call them. Thus, without multiplying examples, we may sum up the result of our studies in the words of Hyatt's Law of Morphogenesis: "A natural classification

may be made by means of a system of analysis in which the individual is the unit of comparison, because its life in all its phases, morphological and physiological, healthy or pathological, embryo, larva, adolescent, adult, and old (ontogeny), correlates with the morphological and physiological history of the group to which it belongs (phylogeny)."

PALÆONTOLOGICAL LABORATORY,
COLUMBIA UNIVERSITY.